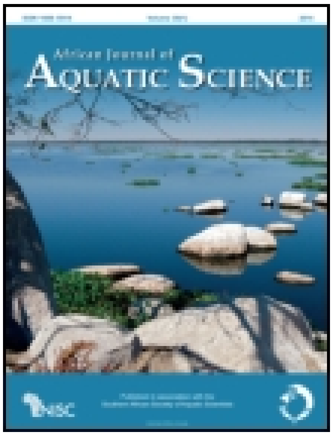

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Predicting the potential distribution of invasive silver carp *Hypophthalmichthys molitrix* in South Africa

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Predicting the potential geographical distribution and spread of non-native species is of major concern to ecologists. Silver carp *Hypophthalmichthys molitrix*, ranked as one of the world's 100 worst invasive species, were introduced into South Africa in 1975, but the potential spread of this invader has not yet been addressed, despite recent studies indicating its potential ecological impacts in South Africa. The potential range of silver carp in South Africa was identified based on ecological niche modelling (ENM) using the maximum entropy method. Models were constructed using occurrence records and a defined background, and calibrated using a *k*-fold method. The area under the receiver operating characteristics curve (AUC) was used to evaluate model performance. Both the native and introduced range model accurately predicted species occurrences (AUC 0.98 and 0.94, respectively). Most of the north-eastern part of South Africa, including the Limpopo River Basin, where the presence of silver carp has been recorded, was correctly predicted as climatically suitable for silver carp. Other areas with suitable climatic conditions for silver carp but with no known introductions were also identified. The model demonstrated the potential use of ENM to predict the potential range of silver carp in South Africa.

Keywords: Asian carp, correlative approach, Cyprinidae, ecological niche modelling, exotic, maximum entropy

Introduction

Invasive species generally disrupt recipient ecosystems, leading to a loss of native biodiversity (Gozlan et al. 2010; Zengeya et al. 2011). Early detection or *a priori* assessment of the invasive potential of non-indigenous species is instrumental in reducing, or even preventing, potential impacts on recipient ecosystems. One method of predicting the potential distribution of species is by means of ecological niche modelling (ENM) (Guisan and Zimmermann 2000). Correlative modelling approaches relate occurrence data to globally available spatial environmental data, summarising abiotic factors limiting the distribution of species (Peterson 2003). An ENM can be used to identify geographical areas with similar abiotic environmental conditions as the realised niche of the species in its native range (Peterson 2003).

The native range of silver carp *Hypophthalmichthys molitrix* (Valenciennes, 1844) (Cyprinidae) extends over most of eastern Asia, including the middle and lower reaches of most major Chinese rivers such as the Yangtze, Pearl and Yellow rivers (Zhang et al. 2001; Chen et al. 2007; Kolar et al. 2007; Hong-Xia et al. 2010). Early intentional translocations and artificial propagation for aquaculture have extended the range of silver carp within their native range, and led to debate about the exact extent of their native range (Chen et al. 2007; Kolar et al. 2007). Silver carp have been widely introduced, and their ability to cause changes in ecosystem structure and functioning is well known (Spataru and Gophen 1985; Irons et al. 2007).

Generally, silver carp require large, low-gradient, turbid rivers with a flow speed of 0.3–0.7 m^{-1} to enable successful propagation (Kolar et al. 2007). However, other studies have found that silver carp are capable of establishing under a wide range of environmental conditions (Spataru and Gophen 1985; Opuszynksi et al. 1989; Lu et al. 2002; Kolar et al. 2007; Calkins et al. 2012; NL unpublished data). This is contrary to the notion that silver carp require specific hydrological conditions to enable their establishment (Linhart et al. 1995; Coulter et al. 2013).

Silver carp are well-known invaders, owing to life-history traits such as their high reproductive rate and fast growth that often lead to high population densities (Sass et al. 2010). Silver carp are also known to be versatile and generalist filter feeders that feed primarily on phytoplankton and zooplankton, but which also consume other food items such as vegetable detritus (Kolar et al. 2007; Rosemberg et al. 2010). Their ability to fine-filter large volumes of water, plus their fast growth rate, high population density obtainable and versatile feeding behaviour, can often lead to the alteration of community structures such as food webs and nutrient cycles in recipient ecosystems (Milstein et al. 1988; Cooke et al. 2009; Gozlan et al. 2010; Ma et al. 2010; Rosemberg et al. 2010). Such changes to phytoplankton, zooplankton and fish community structure can result in decreased size, growth rate, fitness and abundance of native fishes sharing a similar food niche with silver carp

(Spataru and Gophen 1985; Milstein et al. 1988; Lu et al. 2002; Kolar et al. 2007; Sampson et al. 2009). For example, in river systems in North America where silver carp have been introduced, observed dietary overlap between silver carp and indigenous species such as paddlefish *Polyodon spathula*, gizzard shad *Dorosoma cepedianum*, and bigmouth buffalo *Ictiobus cyprinellus*, has been implicated in the decline in condition factor and biomass of these indigenous species (Spataru and Gophen 1985; Irons et al. 2007; Sampson et al. 2009). Silver carp are ranked as one of the 100 worst invasive species in the world by the international Invasive Species Specialist Group (http://www.issg.org/index.html), endorsed by the IUCN Species Survival Commission. Furthermore, in North America the silver carp have been classified as a harmful species under the Injurious Wildlife Provision of the Lacey Act (Act 18 United States Code 42, as amended).

Introduced in 1975, silver carp were the first phytoplanktivorous fish to be introduced into South Africa for algae control, which proved unsuccessful (Prinsloo and Schoonbee 1987). In 1992 silver carp were released into Flag Boshielo Dam on the Olifants River, Mpumalanga, where they successfully established feral populations. These have subsequently spread downstream into the Kruger National Park (Brits 2009). The known extent of the silver carp invasion in South Africa is confined to the Limpopo River Basin (Brits 2009). However, the full extent of the current distribution of the species in South Africa is unknown. Few studies have been undertaken on the invasion biology of silver carp in recipient river systems in South Africa. It has been suggested that silver carp could be associated with the mass mortality events of crocodiles in the Kruger National Park (Woodborne et al. 2012; Huchzermeyer et al. 2013). The trophic ecology of silver carp in the oligotrophic Flag Boshielo Dam has been assessed (NL unpublished data), and preliminary evidence indicates the ability of silver carp to establish in novel environments, despite potential limiting conditions such as a low food resource base due to low primary productivity. Given their potential negative impacts, it is relevant to determine their potential distribution in river systems in South Africa.

This study used niche modelling to predict the potential distribution of silver carp in South Africa. This was achieved by matching environmental conditions associated with the known occurrence of silver carp in their native and introduced ranges to predict potential suitable areas outside their known distribution range where they are likely to establish. The specific objectives were (1) to develop a niche model for silver carp in their native range and to test the accuracy of that model; (2) to project the niche model onto South Africa and evaluate the predictive performance of the model; and (3) to identify areas in South Africa at high risk of invasion, and to discuss conservation implications within South Africa. Predicting the potential geographical range of silver carp in South Africa is necessary in order to identify river segments that are highly susceptible to their establishment. Concerted conservation efforts can then be directed to such areas in order to prevent establishment, direct remediation efforts and contain further spread.

Materials and methods

Occurrence records

Occurrence records for silver carp were sourced from the Global Biodiversity Information Facility (GBIF; http://www.gbif.org; sourced on 05/04/2011) and the Nonindigenous Aquatic Species (NAS) information resource from the United States Geological Survey (USGS; http://nas.er.usgs.gov/queries/CollectionInfo.aspx?SpeciesID=549; sourced on 12/07/2011). All records obtained were examined for errors and records with a spatial resolution greater than 0.05°, as well as duplicates, were removed, leaving 248 occurrence records, including 224 from North America (24.59°–53.79° N, 66.14°–125.02° W), 12 from the native range in eastern Asia, and 12 from South Africa. The larger number of North American records, in comparison to the South African and native range records, resulted in the over-representation of North America in the modelling process. North American records were filtered to 1° spatial resolution to remove the bulk of the records by selecting only one occurrence record per 1° grid cell. Since the remaining 88 occurrence records still over-represented North America in the modelling dataset, 30 occurrence records were randomly selected using the statistical software package R (R Development Core Team 2008) to obtain a relatively even proportion of North American records to the 12 native range and 12 South African records used for modelling.

Bioclimatic variables

A set of 19 globally available bioclimatic variables were sourced from the climate database WorldClim (http://www.worldclim.org; Hijmans et al. 2005) and interpolated at a spatial resolution of $0.05° \times 0.05°$. Bioclimatic variables included those representing annual trends (e.g. mean annual temperature and precipitation); extreme or limiting environmental factors (e.g. mean temperature and precipitation of the driest and wettest quarters); and variables accounting for seasonality (e.g. seasonal temperature and precipitation) for climate data recorded from 1950 to 2000. Bioclimatic variables were evaluated using three criteria: correlation analysis, biological relevance to the species, and a jack-knife procedure. A correlation analysis was used to identify and group highly correlated variables, using a cut-off point of greater than 0.8, following Austin (2002) and Mas et al. (2004). Within each group of correlated variables, only those with a direct effect on the physiological tolerances of silver carp were used as predictors in subsequent analysis. Variables that are known to limit the distribution and survival of silver carp are well documented (Kolar et al. 2007) and, therefore, as suggested by Jiménez-Valverde et al. (2011), response curves obtained from models run using selected variables from the correlation analysis were carefully examined to ensure that they were congruent with the documented physiological tolerances of the silver carp. To avoid spurious overfitting by correlated variables, a jack-knife procedure in the maximum entropy (Maxent) modelling package (Maxent v. 3.2.19; Phillips et al. 2006) was used to assess the contribution of each bioclimatic variable to the model performance. Variables contributing little to the initial model performance were omitted. Four direct predictors out of the initial 19 bioclimatic variables summarising biologically relevant parameters were included in the final model (Table 1).

Fishes are ectothermic and changes in water temperature are therefore likely to affect their biochemical reactions and influence physiological characteristics such as development and growth, as well as ecological and behavioural responses such as the onset of migration and reproduction (Linhart et al. 1995; Chen et al. 2007; Herborg et al. 2007; Buisson et al. 2008; DeVaney et al. 2009). Furthermore, precipitation influences the availability of surface water, habitat, food resources and overall primary productivity (Galloway and Cowling 1978). A fundamental limitation when using ENM to predict the potential distribution of aquatic species is the lack of aquatic environmental data (e.g. water quality variables). However, atmospheric variables have been used successfully as proxies for aquatic environmental data (Iguchi et al. 2004; Zambrano et al. 2006; Chen et al. 2007; Herborg et al. 2007; DeVaney et al. 2009; Zengeya et al. 2013) due to the strong correlation between water and atmospheric temperatures (Caissie et al. 2001).

Table 1: Bioclimatic variables sourced to model the potential distribution of silver carp in South Africa. Highly correlated variables were removed through correlation analysis and a jack-knife procedure. Variables in bold type were included in the modelling process

Bioclimatic variables
Annual mean temperature
Mean diurnal temperature range
Isothermality
Temperature seasonality
Max. temperature of warmest month
Min. temperature of coldest month
Temperature annual range
Mean temperature of wettest quarter
Mean temperature of driest quarter
Mean temperature of warmest quarter
Mean temperature of coldest quarter
Annual precipitation
Precipitation of wettest month
Precipitation of driest month
Precipitation seasonality (coefficient of variation)
Precipitation of wettest quarter
Precipitation of driest quarter
Precipitation of warmest quarter
Precipitation of coldest quarter

Model building

Model building was performed by combining bioclimatic variables and species occurrence records to construct a model of the niche requirements of the species in its native range in eastern Asia, using Maxent. The Maxent method has been shown to perform well in comparison to other approaches that use presence and background data (Elith et al. 2006; Peterson et al. 2007; Elith and Graham 2009; Kearney et al. 2010; Wolmarans et al. 2010). User-specified parameters were set to default, as suggested by Liu et al. (2005), with the regularisation multiplier = 1; maximum number of iterations = 500; convergence threshold = -10^{-5}; and test percentage = 0, with only hinge features selected (Phillips and Dudik 2008). Hinge features, the default setting of Maxent (Phillips and Dudik 2008), are similar to the step function response produced by the 'threshold features', but allow simpler and more concise approximations of the true species response to the environment variables (Elith et al. 2011), thus preventing overfitting of the model without significantly increasing the complexity of models and improving the model performance (Phillips et al. 2006). The recommended logistic transformations of the cumulative probabilities (Phillips et al. 2006) were used, rather than the raw formats, to indicate climatic suitability (Elith et al. 2011). This linear logistic probability indicates the climatic suitability of the areas and not the probability of establishment (Pearson et al. 2007), with values ranging from 0% to 100% (low to high suitability). The analyses were confined to the study region of the species' native range in eastern Asia (Figure 1a) and its potential range in South Africa (Figure 1b).

The maximum entropy method uses occurrence records (representing species presence) and a defined background, representing pseudo-absence, to predict the potential distribution of a species. However, the extent of the background area can influence model performance (VanDerWal et al. 2009; Anderson and Raza 2010). A broad background can cause overestimates and a constrained background can cause underestimates. The background extent should typically encompass the geographical native range of the study species. In this study the native range of silver carp was defined as the area where it is known to occur naturally (18.83°–50.69° N; 96.16°–145.74° E), as defined by Chen et al. (2007). We further delimited the background within this region by using only areas that had similar climates to known silver carp occurrence records. This was achieved by overlaying the Köppen–Geiger climate classification system (Kottek et al. 2006) with the defined silver carp native range, following Thompson et al. (2011). The Köppen–Geiger polygons identify areas with similar climates (climate zones) and a given climate zone was included as part of the background if it contained an occurrence record within the native range of silver carp, using ArcGIS® v. 10.0 (2011; ESRI, Redlands, California) (Figure 1a). By selecting the entire climatic zone, an intermediate background size was obtained, compensating for the few native occurrence records obtained and capturing the expected distribution of the silver carp in their native range (VanDerWal et al. 2009; Jiménez-Valverde et al. 2011).

The native range model was then calibrated with 10 000 pseudo-absence points drawn at random from the defined native background (Phillips et al. 2009; VanDerWal et al. 2009). Native occurrence records were partitioned into a calibration set (training set) and a testing set (validation set) using *k*-fold partitioning (Phillips et al. 2006). This method divides occurrence records into *k* datasets and, for each of the iterations, $k-1$ datasets are pooled for model calibration, while the remaining set is used for model evaluation (Phillips et al. 2006). Average model performance was obtained by repeating the process for 10 iterations. A consensus map was then created as an average of the

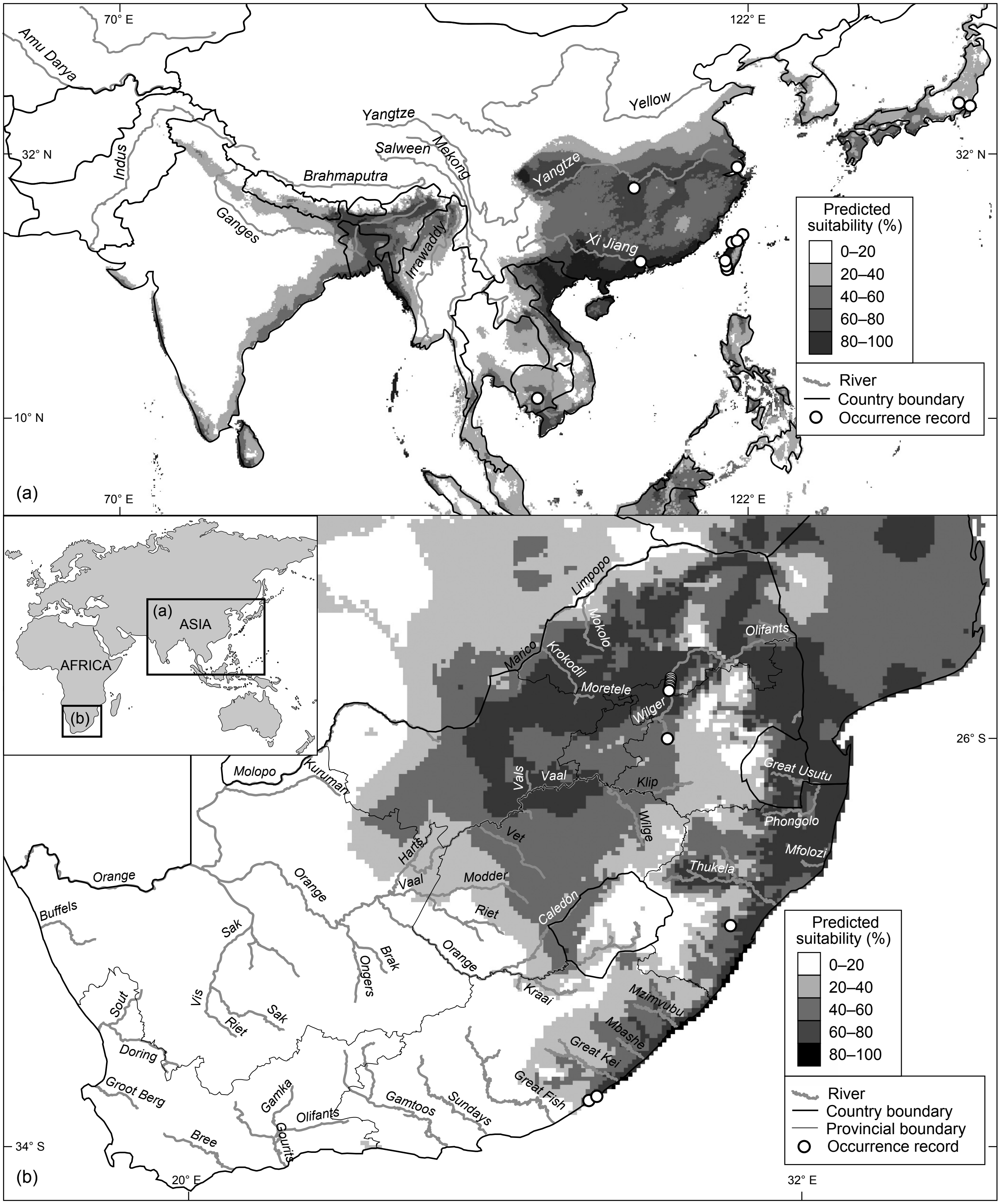

Figure 1: Spatially explicit predictions of potential climatically suitable range of silver carp *Hypophthalmichthys molitrix* in (a) their native range in the south Asian subcontinent, and (b) South Africa

10 native range projection maps. The *k*-fold method is the preferred method when using as few as five occurrence records (Pearson et al. 2007), as all the available data are used for model calibration and evaluation (Fielding and Bell 1997; Jiménez-Valverde et al. 2011).

The introduced range model of silver carp in South Africa was built using known introduction records from South Africa and North America and native range occurrence records in eastern Asia. The introduced range model was then calibrated using the same *k*-fold method as outlined for the native range model (Phillips et al. 2006), while the background selection was restricted to the native range. The combination of the native and introduced occurrence records in model building enhances model performance (Iguchi et al. 2004; Broennimann and Guisan 2008; Beaumont et al. 2009; Liu et al. 2011). This approach provides a better approximation of the invasive species' fundamental niche, as it includes climatic conditions in disjunct native and introduced ranges that may show variation in environmental variables because of the landscape heterogeneity (Jiménez-Valverde et al. 2011).

Model evaluation

A receiver operating characteristic curve (ROC) (Swets 1988) was used to test the performance of the niche models of silver carp from its native and introduced ranges (Iguchi et al. 2004). The ROC curve plots the correctly classified occurrence records (sensitivity) against the incorrectly classified occurrences (1 − specificity) for all possible thresholds, and distinguishes between omission (i.e. predicted absent in areas of actual presence) and commission errors (i.e. predicted presence in areas of actual absence) (Fielding and Bell 1997). Despite several limitations, such as equal weighting of omission and commission errors (Soberón and Peterson 2005; Jiménez-Valverde 2011), the ROC is widely used as test of model accuracy (Fielding and Bell 1997; Wiley et al. 2003; Iguchi et al. 2004). The ROC curve, as used in Maxent, defines the ability of the model to discriminate between presence records and random background points, and not between presence and absence records, since Maxent does not make use of absence data (Fielding and Bell 1997; Phillips et al. 2006).

The area under the curve (AUC) of a ROC curve provides a single measure of model performance, independent of any particular threshold chosen, with the AUC values ranging from 0 to 1 (Phillips et al. 2006). An AUC score of <0.8 indicates poor model discrimination between presence and random background records, 0.8–0.9 indicates models with fair accuracy; 0.9–0.95 indicates a good model; and models with excellent accuracy typically have an AUC score of >0.95 (Thuiller et al. 2006).

Results

Native range model

A high probability of climatic suitability (>60%) corresponded to accurate model prediction of occurrence records in the native range in the lower and middle reaches of the Yangtze River (Figure 1a). Over replicated runs, the mean AUC value was higher for the calibration dataset (0.986; SD 0.002) than for the testing dataset (0.975; SD 0.028), indicating excellent model performance. Rainfall, optimally >1 000 mm y^{-1}, was highlighted as the most important variable for climate suitability. Precipitation of the warmest quarter contributed 36% to the model, and annual precipitation contributed 27.9%. Areas with a large mean diurnal range, i.e. the mean difference in the daily maximum temperature and the minimum temperature, were predicted to be less climatically suitable (<45%). The mean temperature of the warmest quarter contributed the least to the model (13.9%).

Introduced range model

The mean AUC score observed for the testing dataset (0.944; SD 0.031) and calibration dataset (0.957; SD 0.002) of the introduced range model, over replicated runs, indicated excellent model performance. The predicted invasive potential of silver carp revealed an extensive area of high climatic suitability (>70%; Figure 1b). The climatically suitable area identified stretches over most of the north-eastern part of South Africa, which includes the Limpopo, Gauteng and North-West provinces, and areas along the KwaZulu-Natal (KZN) coast (Figure 1b), extending north into Mozambique and Zimbabwe. The major river systems within this potential distribution are the Limpopo, most of the Vaal and the Thukela. The model predicted a low climatic suitability (<30%) in the lower Orange River, Western Cape, Northern Cape and the Vaal River in the western Free State province. A slightly higher (<40%), but still relatively low, climatic suitability was predicted in the central part of Mpumalanga province. The area of highest climatic suitability was that at the convergence of the Gauteng, Limpopo and North-West provincial boundaries (Figure 1b). The precipitation of the warmest quarter contributed 59.2% to the model, suggesting high climatic suitability if there is high rainfall (optimum >400 mm) during the warmest quarter. The mean temperature of the warmest quarter contributed 31.7%, and the associated response curves indicated that temperatures below 10 °C or above 36 °C are not climatically suitable. The optimum temperature for silver carp is predicted to range between 23 and 28 °C. Annual precipitation contributed 6% to the model and indicted optimal suitability in high-rainfall areas (>800 mm y^{-1}).

Discussion

Native range predictions

The high AUC values indicated excellent model performance (>0.95) with accurate predictions of known occurrence records. The predicted native range from this study agreed with the known native range of silver carp (Chen et al. 2007; Kolar et al. 2007; Hong-Xia et al. 2010; Tan et al. 2010). The predicted native range included the middle and lower reaches of the Yangtze River (Kolar et al. 2007), and of other rivers such as the Yellow, Lijiang, Mekong and Pearl river systems in eastern Asia. Areas predicted were mostly high-rainfall areas such as, for example, rainforest, with the drier, deciduous forest areas being predicted with low probabilities (<50%). The presence of introduced silver carp populations that have been recorded in the Brahmaputra River Basin in India and Bangladesh (Hoque 1995) was also accurately predicted as being climatically suitable in this study. The native range of silver carp predicted in the present study is comparable with that of previous studies, despite the use of different approaches. Previous studies (Chen et al. 2007; Herborg et al. 2007) predicted the invasive potential of silver carp in North America using the Genetic Algorithm for Rule-set Prediction (GARP) software (Stockwell and Peters 1999) and used a larger dataset (>100) of native occurrence records and more environmental variables than used in this study. This study produced similar native range predictions despite using only 12 native occurrence records and a different modelling approach. The maximum entropy modelling approach has been shown to outperform other modelling approaches (Elith et al. 2006; Poulos et al. 2012) and can be used to predict the realised native distribution range of silver carp in conjunction with the carefully delineated background and limited occurrence records, despite only a few native occurrence records being available for model building (Figure 1a).

Introduced range predictions

Large areas of north-eastern South Africa were predicted as climatically suitable for the establishment of silver carp. Areas where silver carp have already established feral populations in South Africa, such as the Olifants River, Limpopo province, had a high predicted climatic suitability (>0.75%). Of particular concern are those areas that have been free of silver carp, but that were predicted to be potentially suitable for its establishment. These include the Steelpoort and the upper Olifants rivers in the Limpopo drainage basin, where a high (>80%) climatic suitability for silver carp establishment was predicted. In addition, the coast of KwaZulu-Natal, especially the whole of the Thukela River (>0.75%), and parts of the Vaal River were also found to be climatically suitable (Figure 1b).

Precipitation of the warmest quarter was the most important bioclimatic variable identified. Silver carp have specific spawning habitat requirements (Kolar et al. 2007) and areas with the highest predicted climatic suitability were generally areas with high annual rainfall, particularly during the warmest quarter of the year. As expected, low rainfall and winter rainfall areas were not predicted, since silver carp require peak river discharge during the onset of the warmest quarter of the year for successful reproduction (Linhart et al. 1995; Kolar et al. 2007). In North America, annual precipitation and wet-day frequency were identified as the major factors influencing the potential spread of silver carp (Herborg et al. 2007). The suitable temperature range, detected by the response curves obtained from the model in the current study, coincides with the observed thermal tolerance range of the species of 24–34 °C, which is considered optimal for growth and reproduction (Kolar et al. 2007; Cooke and Hill 2010). The response curves also indicated a sudden decrease in suitability when temperature exceeded the species' thermal tolerance level (<36 °C). The optimal water temperature range of silver carp, 30–34 °C in summer and 22–26 °C in winter (FAO 2004), was consistent with the subtropical to tropical climate found in the north-eastern part of South Africa and along the east coast, which were predicted to be climatically suitable areas for the establishment of silver carp.

Conservation concerns

Silver carp have already established feral populations in the middle reaches of the Olifants River. They have spread downstream and are now common in river systems in the Kruger National Park, a flagship conservation area in South Africa, and in Massingir Dam, Mozambique (Brits 2009). A large proportion of river systems that are still free of silver carp were predicted to have a similar climate to that of the native range of silver carp. This implies that, if silver carp were introduced into such river systems, they may be able to become established, other factors notwithstanding, such as biotic interaction with native species.

The present distribution and potential geographical range predicted for silver carp in South Africa encompass the native range of several indigenous species that are at an extirpation risk as a result of the silver carp invasion. The impact of silver carp in the Olifants River is yet to be quantified, though preliminary results from a parallel ongoing study in Flag Boshielo Dam have shown strong niche overlap between silver carp and indigenous species such as banded tilapia *Tilapia sparrmanii*, silver robber *Micralestes acutidens*, redeye labeo *Labeo cylindricus*, threespot barb (*Barbus trimaculatus*) and rednose labeo (*Labeo rosae*) (NL unpublished data). Silver carp have also exhibited opportunistic and versatile feeding strategies, being able to switch between food sources and to consume whatever is available. These strong niche overlaps can lead to a decrease in the abundance of indigenous fish sharing a similar dietary niche, and the dietary plasticity of silver carp may aid its establishment.

What can be done to control and prevent further spread?

The adverse ecological impacts on recipient freshwater ecosystems worldwide associated with fish introductions have drawn attention to the need to control and manage the movement of invasive species. In response to this threat, most countries have implemented legislation prohibiting new introductions and some have developed adaptive management strategies to identify and minimise the impact of invasive species. In South Africa, invasive species are regulated through the alien and invasive species regulations of the National Environmental Management: Biodiversity Act (NEM:BA; RSA 2004). Silver carp are currently listed in section 70(1) (a) category 1b, which means that this species requires control by means of an invasive species management programme. At present there is no invasive species management plan for silver carp in South Africa. Recommendations follow for the formulation of such a management plan, in line with section 76 of NEM:BA. The framework of the proposed management plan should include actions to prevent further introductions, the establishment of early detection monitoring and a rapid response plan for new introductions, as well as plans to mitigate the impacts of existing populations by reducing their abundance and minimising spread.

Prevention

Once established, invasive fish species are difficult to eradicate, and therefore management protocols that focus on preventing introductions should be encouraged, these often being much easier and cheaper to implement.

Ecological risk assessments have been widely used as a screening tool to identify potential invasive species and to assess the risk of adverse ecological impacts on ecosystem structure and functioning associated with the establishment and spread of a given species (National Research Council 2002). The authors are not aware of any risk assessment that has been done for silver carp in South Africa. It is envisaged that the niche model outlined in this study will provide the information required to undertake such a comprehensive risk assessment for silver carp. The background information used to construct the niche model includes information on the climate and geographic extent of the native range, dispersal mechanism, undesirable traits, history of introductions and the extent of naturalisation of silver carp. Further, human-facilitated movement of silver carp for the biological control of phytoplankton was identified as an import driver of its introduction into South Africa. There is, therefore, a need to raise public awareness of the potential impact of silver carp in recipient areas to prevent further introductions and, especially, translocations from the Olifants River.

Invasive species monitoring – early detection and rapid response

According to section 76 of the NEM:BA, all relevant management authorities of protected areas and organs of state in all spheres of government are required to provide invasive species monitoring, control and eradication plans. Monitoring plans should provide for early detection, assessment and rapid response to prevent or to slow invasions. Early detection requires the provision of easily accessible information platforms where the general public and concerned stakeholders can report the possible occurrence of invasive species. For example, in South Africa there is a large angling community that can aid in the timely reporting of unrecorded occurrences of invasive fish species, and can also provide information on the illegal introduction and stocking of invasive fish species. If an invasive species is detected or reported, the relevant authorities can then confirm its establishment and can record its occurrence in a national register of invasive species. The species information database will then provide data that can be used in planning and conservation activities. The niche model illustrates one potential use of invasive species occurrence databases. The model highlights areas with known introductions of silver carp and the extent silver carp invasion, and provides an opportunity to identify regions in South Africa that are climatically suitable for the establishment of silver carp and which should be monitored for early detection. It also helps identify areas were indigenous species and ecosystems might be at risk from silver carp invasion. Further, in areas that are still free of silver carp, but which the niche model predicts to be suitable, regular monitoring would determine if the species is invading and would also assist in identifying introduction pathways.

Control and eradication

The eradication of silver carp in the Olifants River is now probably impractical because of the large spatial extent of their invaded range and the large population densities attained in reservoirs such as Flag Boshielo and Massingir dams. Furthermore, the use of classical biological and chemical control measures for such a widespread invasive fish species are not effective management options because they tend to be non-target-specific and may affect the indigenous fish fauna in recipient areas (Gozlan et al. 2010). The only practical management option is to predict the species' potential distributional range and to adopt measures to slow down its dispersal across river systems. In the case of the silver carp, the niche model presented in this study outlines this species' potential invasive range and the following measures can be used to restrict it to catchments where it has already established and to prohibit its introduction into river catchments where it has not invaded.

The spread of silver carp into the upper Olifants catchment is probably limited by its highly seasonal surface water flows and physical barriers such as dam and weirs. Barriers such as weirs may act as short-term management options to prevent upstream migration of invasive fishes (Rahel 2013), but their efficacy can be reduced by episodic flood events, which may enable silver carp to move upstream when the water level is high enough for them to clear low weirs. However, larger dams >15 m high, such as Loskop Dam, act as permanent barriers to the natural upstream spread of the silver carp in the Olifants River. Targeted removal of silver carp is also advocated as an effective management option under NEM:BA, where catch-and-release of silver carp is prohibited in protected and fish sanctuary areas such as national parks, provincial reserves and mountain catchments areas. The spread of silver carp can also be prevented through legislation. For example, silver carp are listed in section 70(1)(a) category 1b, which prohibits the import of silver carp into South Africa. For existing feral populations, the use silver carp for any commercial purposes and their translocation and introduction into river catchments that are still free of silver carp are prohibited. The effective implementation of this policy will, however, depend largely on the engagement and cooperation of all concerned stakeholders.

This study takes cognisance of the fact that the spread of silver carp in river systems in South Africa may also be influenced by other conditions that were not considered in the niche model. These include spawning habitat requirements, food availability and biotic interactions with native species.

Conclusions

The model performance demonstrated that potential distributions of invasive species can be accurately predicted using few occurrence records, a minimal number of carefully selected bioclimatic variables and a carefully defined background. The model presented in this study can be used for informing management plans and guiding monitoring efforts in preventing the potential further spread of silver carp in South Africa. Eradication of this species from South Africa may not be feasible, but limiting its further spread is crucial for conserving the region's freshwater aquatic systems.

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References

Anderson RP, Raza A. 2010. The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: preliminary tests with montane rodents (genus *Nephelomys*) in Venezuela. *Journal of Biogeography* 37: 1378–1393.

Austin MP. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling* 157: 101–118.

Beaumont LJ, Gallagher RV, Thuiller W, Downey PO, Leishman MR, Hughes L. 2009. Developing climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions. *Diversity and Distributions* 15: 409–420.

Broennimann O, Guisan A. 2008. Predicting current and future biological invasions: both native and invaded ranges matter. *Biological Letters* 4: 585–589.

Brits DL. 2009. Distribution of the silver carp, *Hypophthalmichthys molitrix* (Valenciennes, 1844), in the Flag Boshielo Dam (Arabie Dam) and its potential influences on the ecology of the dam. PhD thesis, University of Limpopo, South Africa.

Buisson L, Thuiller W, Lek S, Lim P, Grenouillet GL. 2008. Climate change hastens the turnover of stream fish assemblages. *Global Change Biology* 14: 2232–2248.

Caissie D, El-Jabi N, Satish MG. 2001. Modelling of maximum daily water temperatures in a small stream using air temperatures. *Journal of Hydrology* 251: 14–28.

Calkins HA, Tripp SJ, Garvey JE. 2012. Linking silver carp habitat selection to flow and phytoplankton in the Mississippi River. *Biological Invasions* 14: 949–958.

Chen P, Wiley EO, McNyset KM. 2007. Ecological niche modelling as a predictive tool: silver and bighead carps in North America. *Biological Invasions* 9: 43–51.

Cooke SL, Hill WR. 2010. Can filter-feeding Asian carp invade the Laurentian Great Lakes? A bioenergetic modelling exercise. *Freshwater Biology* 55: 2138–2152.

Cooke SL, Hill WR, Meyer KP. 2009. Feeding at different plankton densities alters invasive bighead carp (*Hypophthalmichthys nobilis*) growth and zooplankton species composition. *Hydrobiology* 625: 185–193.

Coulter AA, Keller D, Amberg JJ, Bailey EJ, Goforth RR. 2013. Phenotypic plasticity in the spawning traits of bigheaded carp (*Hypophthalmichthys* spp.) in novel ecosystems. *Freshwater Biology* 58: 1029–1037.

DeVaney SC, McNyset KM, Williams JB, Peterson AT, Wiley EO. 2009. A tale of four 'Carp': invasion potential and ecological niche modelling. *PLoS ONE* 4: e5451.

Elith J, Graham CH. 2009. Do they? How do they? Why do they differ? On finding reasons for differing performances of species distribution models. *Ecography* 32: 66–77.

Elith J, Graham CH, Anderson RP, Dudík M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JMC, Peterson AT, Phillips SJ, Richardson KS, Scachetti-Pereira R, Schapire RE, Soberón J, Williams S, Wisz MS, Zimmermann NE. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29: 129–151.

Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ. 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* 17: 43–57.

FAO (Food and Agriculture Organization). 2004. Drought impact mitigation and prevention in the Limpopo River Basin. A situation analysis. *Land and water discussion paper* No. 4. Rome. FAO Subregional Office for Southern and East Africa, Harare. Available at ftp://ftp.fao.org/agl/aglw/docs/lwdp4_e.pdf [accessed 11 November 2011].

Fielding AH, Bell JF. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24: 38–49.

Galloway JN, Cowling EB. 1978. The effects of precipitation on aquatic and terrestrial ecosystems: a proposed precipitation chemistry network. *Journal of the Air Pollution Control Association* 28: 229–235.

Gozlan R, Britton JR, Cowx I, Copp GH. 2010. Current knowledge on non-native freshwater fish introductions. *Journal of Fish Biology* 44: 751–786.

Guisan A, Zimmermann NE. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135: 147–186.

Herborg L, Mandrak NE, Cudmore BC, MacIsaac HJ. 2007. Comparative distribution and invasive risk of snakeheads (Channidae) and Asian carp (Cyprinidae) species in North America. *Canadian Journal of Fisheries and Aquatic Sciences* 64: 1723–1735.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978.

Hong-Xia Y, Wen-Qiao T, Si-Fa L. 2010. Morphological changes of silver and bighead carp in the Yangtze River over the past 50 years. *Zoological Research* 31: 651–656.

Hoque MT. 1995. Sustainable agriculture: a perspective on fish culture for the small-scale resource-poor farmers of Bangladesh. *Journal of Sustainable Agriculture* 5: 97–112.

Huchzermeyer KDA, Osthoff G, Hugo A, Govender D. 2013. Comparison of the lipid properties of healthy and pansteatitis-affected African sharptooth catfish, *Clarias gariepinus* (Burchell), and the role of diet in pansteatitis outbreaks in the Olifants River in the Kruger National Park, South Africa. *Journal of Fish Diseases* 36: 897–909.

Iguchi K, Matsuura K, McNyset KM, Peterson T, Scachetti-Pereira R, Powers KA, Vieglais DA, Wiley EO, Yodo T. 2004. Predicting invasions of North American basses in Japan using native range data and a genetic algorithm. *Transactions of the American Fisheries Society* 133: 845–854.

Irons KS, Sass GG, McCelland MA, Stafford JD. 2007. Reduced condition factor of two native fish species coincident with invasion of non-native Asian carps in the Illinois River, U.S.A. Is this evidence for competition and reduced fitness? *Journal of Fish Biology* 71: 258–273.

Jiménez-Valverde A. 2011. Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modelling. *Global Ecology and Biogeography* 21: 498–507.

Jiménez-Valverde A, Peterson AT, Soberón J, Overton JM, Aragón P, Lobo JM. 2011. Use of niche models in invasive species risk assessment. *Biological Invasions* 13: 2785–2797.

Kearney MR, Wintle BA, Porter WP. 2010. Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conservation Letters* 3: 203–213.

Kolar CS, Chapman DC, Courtenay WR, Housel CM, Williams JD, Jennings DP. 2007. Bigheaded carps: a biological synopsis and environmental risk assessment. *American Fisheries Society Special Publication* 33. Bethesda, Maryland: American Fisheries Society.

Kottek M, Grieser J, Beck C, Rudolf B, Rubel F. 2006. World map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift* 15: 259–263.

Linhart O, Kudob S, Billard R, Slechtad V, Mikodina EV. 1995.

Morphology, composition and fertilization of carp eggs: a review. *Aquaculture* 129: 75–93.

Liu C, Berry PM, Dawson TP, Pearson RG. 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* 28: 385–393.

Liu X, Guo Z, Ke Z, Wang S, Li Y. 2011. Increasing potential risk of a global aquatic invader in Europe in contrast to other continents under future climate change. *PLoS ONE* 6: e18429.

Lu M, Xie P, Tang H, Shao Z, Xie L. 2002. Experimental study of trophic cascade effect of silver carp (*Hypophthalmichthys molitrix*) in a subtropical lake, Lake Donghu: on plankton community and underlying mechanisms of changes of crustacean community. *Hydrobiologia* 487: 19–31.

Ma H, Cui F, Liu Z, Fan Z, He W, Yin P. 2010. Effect of filter-feeding fish, silver carp, on phytoplankton species and size distribution in surface water: a field study in water works. *Journal of Environmental Sciences* 22: 161–167.

Mas JF, Puig H, Palacio JL, Sosa-López A. 2004. Modelling deforestation using GIS and artificial neural networks. *Environmental Modelling and Software* 19: 461–471.

Milstein A, Hepher B, Teltch B. 1988. The effect of fish species combinations in fishponds on plankton communities. *Aquaculture and Fisheries Management* 19: 127–137.

National Research Council. 2002. *Predicting invasions of non-indigenous plants and plant pests*. Washington, DC: National Academic Press.

Opusynski K, Lirski A, Myszkowski L, Wolnkicki J. 1989. Upper lethal and rearing temperatures for juvenile common carp, *Cyprinus carpio* L. and silver carp, *Hypophthalmichthys molitrix* (Valenciennes). *Aquaculture and Fish Management* 20: 287–294.

Pearson RG, Raxworthy CJ, Nakamura M, Peterson AT. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography* 34: 102–117.

Peterson AT. 2003. Predicting the geography of species' invasion via ecological niche modelling. *Quarterly Review of Biology* 78: 419–433.

Peterson AT, Papes M, Eaton M. 2007. Transferability and model evaluation in ecological niche modelling: a comparison of GARP and Maxent. *Ecography* 30: 550–560.

Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modelling of species geographic distributions. *Ecological modelling* 190: 231–259.

Phillips SJ, Dudik M. 2008. Modelling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31: 161–175.

Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A, Leathwick J, Ferrier S. 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications* 19: 181–197.

Poulos HM, Chernoff B, Fuller PL, Butman D. 2012. Ensemble forecasting of potential habitat for three invasive fishes. *Aquatic Invasions* 7: 59–72.

Prinsloo JF, Schoonbee HJ. 1987. Investigations into the feasibility of a duck-fish-vegetable integrated agriculture-aquaculture system for developing areas in South Africa. *Water SA* 13: 109–118.

Rahel FJ. 2013. Intentional fragmentation as a management strategy in aquatic systems. *BioScience* 63: 362–372.

R Development Core Team. 2008. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.

Rosemberg FM, Attayde J, Vasconcelos FR. 2010. Effects of omnivorous filter-feeding fish and nutrient enrichment on the plankton community and water transparency of a tropical reservoir. *Freshwater Biology* 55: 767–779.

RSA (Republic of South Africa). 2004. National Environmental Biodiversity Act (Act No. 10 of 2004). *Government Gazette, South Africa* 467(26436).

Sampson SJ, Chick JH, Pegg MA. 2009. Diet overlap among two Asian carp and three native fishes in backwater lakes on the Illinois and Mississippi rivers. *Biological Invasions* 11: 483–496.

Sass GG, Cook TR, Irons KS, McClelland MA, Michaels NN, O'Hara TM, Stroub MR. 2010. A mark-recapture population estimate for invasive silver carp (*Hypophthalmichthys molitrix*) in the La Grange Reach, Illinois River. *Biological Invasions* 12: 433–436.

Soberón J, Peterson AT. 2005. Interpretation of models of fundamental ecological niches and species distributional areas. *Biodiversity Informatics* 2: 1–10.

Spataru P, Gophen M. 1985. Feeding behaviour of silver carp *Hypophthalmichthys molitrix* (Val.) and its impact on the food web in Lake Kinneret, Israel. *Hydrobiologia* 120: 53–61.

Stockwell DRB, Peters DP. 1999. The GARP modelling system: problems and solutions to automated spatial prediction. *International Journal of Geographic Information Systems* 13: 143–158.

Swets JA. 1988. Measuring the accuracy of diagnostic systems. *Science* 3: 1285–1293.

Tan XC, Li XH, Lek S, Li YF, Wang C, Li J, Luo JR. 2010. Annual dynamics of the abundance of fish larvae and its relationship with hydrological variation in the Pearl River. *Environmental Biology of Fishes* 88: 217–225.

Thompson GD, Robertson MP, Webber BL, Richardson DM, le Roux JJ, Wilson JRU. 2011. Predicting the subspecific identity of invasive species using distribution models: *Acacia saligna* as an example. *Diversity and Distributions* 17: 1001–1014.

Thuiller W, Broennimann O, Hughes G, Alkemades JRM, Midgley G, Corsi F. 2006. Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. *Global Change Biology* 12: 424–440.

VanDerWal J, Shooa LP, Graham C, Williams SE. 2009. Selecting pseudo-absence data for presence-only distribution modelling: How far should you stray from what you know? *Ecological Modelling* 220: 589–594.

Wiley EO, McNyset KM, Peterson AT, Robins CR, Stewart AM. 2003. Niche modelling and geographic range predictions in the marine environment using a machine-learning algorithm. *Oceanography* 16: 120–127.

Wolmarans R, Robertson MP, van Rensburg BJ. 2010. Predicting invasive alien plant distributions: how geographical bias in occurrence records influences model performance. *Journal of Biogeography* 37: 1797–1810.

Woodborne S, Huchzermeyer KDA, Govender D, Pienaar DJ, Hall G, Myburgh JG, Deacon AR, Venter J, Lübcker N. 2012. Ecosystem change and the Olifants River crocodile mass mortality events. *Ecosphere* 3: 1–17.

Zambrano L, Martinez-Meyer E, Menezes N, Peterson AT. 2006. Invasive potential of common carp (*Cyprinus carpio*) and Nile tilapia (*Oreochromis niloticus*) in American freshwater systems. *Canadian Journal of Fisheries and Aquatic Sciences* 63: 1903–1910.

Zengeya TA, Booth AJ, Bastos ADS, Chimimba CT. 2011. Trophic interrelationships between exotic Nile tilapia, *Oreochromis niloticus*, and indigenous tilapiine cichlids in a subtropical African river system (Limpopo River, South Africa). *Environmental Biology of Fishes* 92: 479–489.

Zengeya TA, Robertson MP, Booth AJ, Chimimba CT. 2013. Ecological niche modeling of the invasive potential of Nile tilapia *Oreochromis niloticus* in African river systems: concerns and implications for the conservation of indigenous congenerics. *Biological Invasions* 15: 1507–1521.

Zhang SM, Deng H, Wang D, Yu LN. 2001. Population structure and gene diversity of silver carp and grass carp from populations of the Yangtze River systems revealed by random amplified polymorphic DNA. *Acta Hydrobiologica Sinica* 25: 255–330.

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